LATE CENOZOIC BATS (SUBFAMILY NYCTOPHYLINAE) FROM THE ANZA-BORREGO DESERT OF CALIFORNIA

BY

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In the summer of 1967 almost six tons of matrix were washed using modifications of the techniques originated by Hibbard (1949) and McKenna (1962). The matrix was obtained from 15 sites in that part of the Palm Spring Formation (Dibblee, 1954; Woodring, 1931; and Woodard, 1963) in the Fish Creek-Vallecito Creek areas in the Anza-Borrego Desert State Park, San Diego County, California. Washing was done under the auspices of the Los Angeles County Museum of Natural History and supervised by Theodore Downs and George J. Miller. Locality LACM 6583 proved to be especially rich in small vertebrate bones, and except for one specimen from locality LACM 6552, it is from this site that all specimens discussed herein were recovered.

I thank Theodore Downs for his continued support, advice, and encouragement. David E. Fortsch and George J. Miller critically read the manuscript. I am indebted to J. Knox Jones, Jr., and Richard G. Van Gelder for valuable suggestions, including the providing of clues to the literature on Recent *Antrozous*, and to Lisa A. Hansen, who made the illustrations. The cooperation of the personnel and management of the Anza-Borrego Desert State Park is gratefully acknowledged. This research was supported by the National Science Foundation under grant GB-5116. For permission to use comparative specimens I thank J. Knox Jones, Jr., Museum of Natural History, University of Kansas (KU), Richard G. Van Gelder, American Museum of Natural History (AMNH), and Edson Fichter, Idaho State University Museum (ISUM). Theodore Downs and J. R. Macdonald, Los Angeles County Museum of Natural History (LACM) made the fossil bat material available for study. Measurements of specimens were made with a Gaertner measuring microscope to the nearest micron. Symbols used here to identify individual teeth are as follows: in the upper half of the dentition individual teeth are identified with capital letters and numbers, thus I2 refers to the upper second incisor; teeth in the lower half of the dentition are identified with lower case letters and numbers, thus

i3 refers to the third lower incisor; L or R indicates left or right side of the jaw.

The genus *Antrozous* is currently subdivided into two subgenera —*Antrozous* and *Bauerus* (Van Gelder, 1959). There are two species in the former (*A. pallidus* and *A. koopmani*), which are closely related (Orr and Silva Taboada, 1960), and only one species in *Bauerus* (*A. dubiaquercus*).

The nyctophiline bats from the early Pleistocene of the Anza-Borrego Desert are morphologically distinct from the two currently recognized subgenera in North America to the same extent that these two differ from one another. It is for this reason and on data presented subsequently in this paper, that a new genus is here established, and *Bauerus* is regarded as a genus distinct from *Antrozous*.

Anzanycteris, new genus
figures 1-5

Type species.—*Anzanycteris anzensis* (new species).

Diagnosis.—Mandible with i1 and i2 crowded together, i2 markedly reduced, with simple crown, and appressed into indentation near base of lower canine; angular process slender and projecting almost horizontally and posteriad; weakly developed cingulum on lingual edge of C-M3.

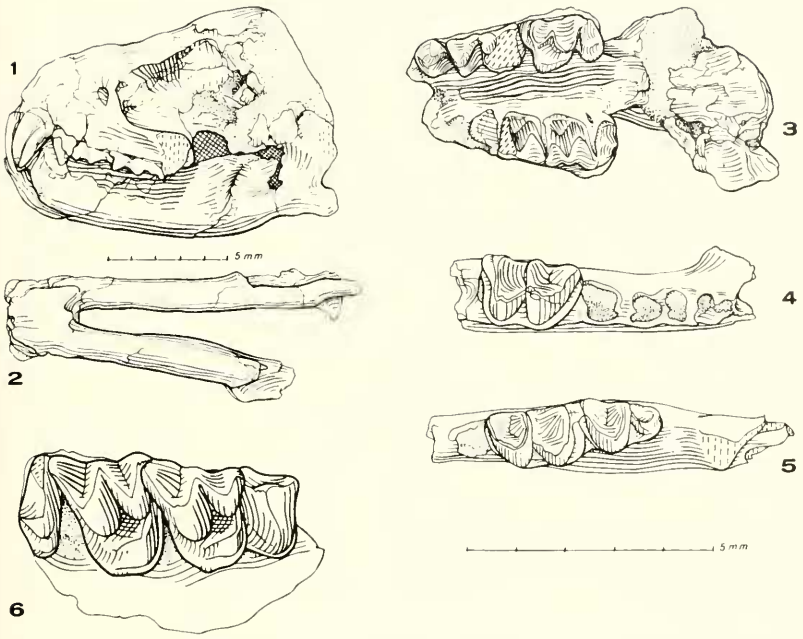
Anzanycteris anzensis, new species

Holotype.—LACM 19300, skull with jaws in articulation, with posterior part of cranium missing from the postglenoid process posteriad; skull crushed laterally; a left-lateral and two medial incisors missing from mandible; alveoli for missing incisors visible.

Diagnosis.—Same as for the genus.

Type locality and stratigraphy.—Locality LACM 6583, Upper Tapiado Wash, Badlands in Anza-Borrego Desert State Park, San Diego County, California; approximately 4850 feet (1478 meters), stratigraphically below top of Palm Spring Formation in the Diablo member of the formation; late Blancan (early Pleistocene) in age, Arroyo Seco Fauna.

Referred specimens.—Topotypes: LACM 19301, fragmentary cranium with incisors and right canine missing, RP4 and LM1 broken, posterior end of cranium missing, fragmentary right petrous portion of inner ear imbedded in the matrix near forward end of braincase; LACM 19303, maxillary fragment with RM2 and broken RM1; LACM 19304, fragmentary left dentary with m2 and broken m1 and m3; LACM 19305, fragmentary right dentary with m2, alveoli for c, p3, p4, and m1, and mental foramen; LACM 19306, fragmentary right dentary with m3, ventral part of masseteric fossa, and dentary foramen; LACM 19307, fragmentary left dentary with m2, m3, and ventral part of masseteric fossa; LACM 19309 fragmentary left dentary with m2 and m3; LACM 19515, Lm1 or Lm2; LACM 19516, fragmentary left dentary with m1 and broken p4 and m2. Locality LACM 6552: LACM 19308, fragmentary left dentary with m2 and m3.



Figs. 1-6. *Anzanycteris anzensis* new genus and species. 1, left lateral view of skull (holotype); 2, ventral view of mandibles (holotype); 3, ventral view of cranium (LACM 19301); 4, dorsal view of right mandibular fragment with m2 (LACM 19305); 5, dorsal view of left mandibular fragment with m2-m3 (LACM 19307); 6, cf. *Anzanycteris* sp., ventral view of right maxillary fragment with P4-M3 (LACM 19302). The short scale refers to Figs. 1-3, the long scale to Figs. 4-6.

Specimens used in comparisons.—*Antrozous pallidus.* California: San Bernardino County, KU 63546; Contra Costa County, KU 11373, 11374. Idaho: Idaho County, ISUM 7370; Bannock County, ISUM 7304, 7305. Kansas: Barber County, KU 11179, 76874. Nevada: Churchill County, KU 75891. *Bauerus dubiaquercus.* Nayarit: Tres Marias Islands, AMNH 180841.

Description.—Two incisors (i1 and i2) present, i2 markedly reduced, having a single crown and appressed into an indentation on the medial side near base of the lower canine; this indentation is bounded by the cingulum dorsally and antero-posteriorly. The lower cheekteeth are essentially as in *Antrozous* and *Bauerus*. The coronoid process is oriented almost vertically as in *Antrozous*. The angular process is slender and projects nearly horizontally and posteriorly and approximately parallel to its mate. The masseteric fossa is moderately deepened, the deepest portion antero-ventral. The shafts of the upper incisors are more than half as long as those of the canines, and the roots of the canines and incisors are pressed close together. The spaces between the upper molars are V-shaped, the apices of the V's projecti g laterad. The contact between P4 and M1 is almost parallel, thus leaving no space between them, and the

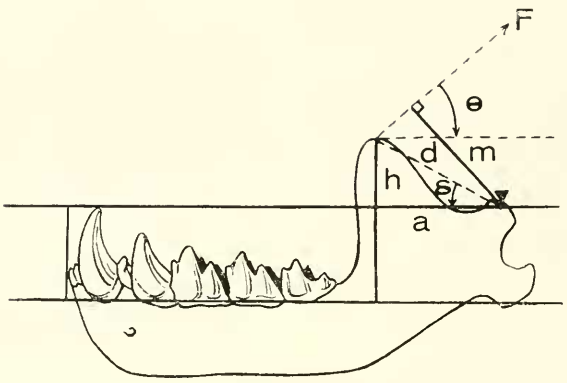


FIG. 7. Left lateral view of the mandible of *Bauerus dubiaquercus* (AMNH 180565), modified from Van Gelder, 1959: fig. 1A. See text for explanation of symbols pertaining to the jaw as a mandibular lever.

canine is closely appressed to the P4. There is no hypocone on M1 and M2, but a loph extends posteriad to the level of the metacone and almost parallel to the longitudinal axis of the palate. The M3 is essentially as in *Antrozous*, as is the infraorbital canal. The upper dentition is probably only slightly upturned as in *Antrozous*. The cingula on the upper cheekteeth are weakly developed when compared to those in *Antrozous* and *Bauerus*.

Comparisons.—In *Anzanycteris* the number of teeth is the same as in *Antrozous* and two less than in *Bauerus* (Van Gelder, 1959). In the latter genus, i3 is a tiny, button-like tooth crowded between i2 and the canine; it is appressed into an indentation on the medial side of the canine. In *Anzanycteris*, i2 is markedly smaller than i1 and is appressed into an indentation on

TABLE 1.—COMPARISONS OF THE STRUCTURES IN THE FOUR GENERA OF THE SUBFAMILY NYCTOPHILINAE, USING CHARACTERS NOTED IN MILLER (1907:235).

Character	*Nyctophilus*	*Bauerus*	*Antrozous*	*Anzanycteris*
Number and character of lower incisors	3, unreduced	3, i3 markedly reduced	2, unreduced	2, i2 markedly reduced
Character of lower canine	Probably "normal"	With excavation	"Normal"	With excavation
Hypocone	Absent	Present	Absent	Absent
M3	More than half crown area of M1 M2	Less than half crown area of M1 M2	Less than half crown area of M1 M2	Less than half crown area of M1 M2
m3	Talonid unreduced	Talonid reduced	Talonid reduced	Talonid reduced
Rostrum	Slightly upturned	Slightly upturned	Slightly downturned	Probably slightly downturned

TABLE 2.—CRANIAL MEASUREMENTS (IN MILLIMETERS) OF *Anzanycteris anzensis* NEW GENUS AND SPECIES AND CF. *Anzanycteris* SP. ALL NUMBERS RELATE TO SPECIMENS IN THE LOS ANGELES COUNTY MUSEUM OF NATURAL HISTORY.

Measurement	No. 19300	No. 19301	No. 19304	No. 19306	No. 19302
Length of maxillary toothrow	5.480	5.882	.....	.....	5.315
Length of infraorbital canal	.349	.....	.....	.....	.....
Depth of mandible at m2	1.948	.....	.....	.....	.....
From posterior end of m3 to posterior end of angular process	5.707	.....	.....	.....	.....
APL at cingulum of C	1.585	1.629	.....	.....	.....
Width at cingulum of C	.....	1.436	.....	.....	.....
APL P4	1.065	1.369	.....	.....	.985
Width P4	.....	1.633	.....	.....	1.824
APL M1	1.847	1.882	.....	.....	1.907
Width M1	.....	1.987	.....	.....	2.294
APL M2	2.108	1.973	.....	.....	1.948
Width M2	.....	2.097	.....	.....	2.539
APL M3	.543	.664	.....	.....	.818
Width M3	.....	1.874	.....	.....	2.043
Width talonid of m1	.....	.....	1.023	.....	.....
APL m2	.....	.....	1.694	.....	.....
Width trigonid of m2	.....	.....	1.164	.....	.....
Width talonid of m2	.....	.....	1.288	.....	.....
APL m3	.....	.....	.....	1.571	.....
Width trigonid of m3	.....	.....	.....	1.032	.....
Width talonid of m3	.....	.....	.448	.447	.....

the medial side near the base of the canine, whereas in *Antrozous* i1 and i2 are subequal in size and the canine has no indentation.

The upper toothrow in *Anzanycteris*, as in *Antrozous*, slopes slightly anterodorsad, whereas in *Bauerus* this upturning of the tooth row is more pronounced or more bulldog-like, and the sagittal crest is far more pronounced.

Because the holotype of *Anzanycteris* has undergone some distortion, presumably during preservation, the degree of upturning of the upper toothrow was determined by assuming the mandibles to move in articulation in a simple, hinge-like, up-and-down motion. The condyloid process has a configuration not unlike that of a canid and the postglenoid process is well developed. Assuming that the latter characteristics of the ma dible would restrict it to a minimal amount of lateral motion, it follows that the temporal muscles would exert the principal force in adducting the mandible while the masseter and pterygoid musculature would function primarily in positioning the mandible with respect to the glenoid fossa.

Using a modification of a technique devised by Ostrom (1966), the center of the glenoid fossa was established as a fulcrum and the coronoid process above the level of the fulcrum as a lever. The mandible was then occluded and the center of origin of the temporal muscles was estimated. A line was then drawn from the tip of the coronoid process to the center of origin of the temporal muscles. Using these data the moment arm of the applied force

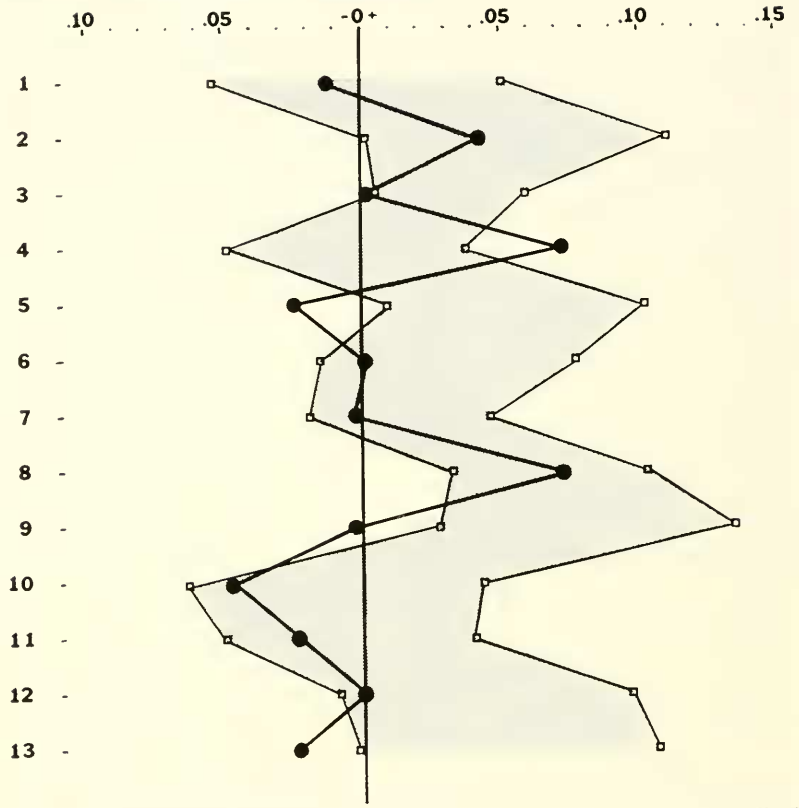


FIG. 8. Ratio diagrams modified from Simpson *et al.* (1960), comparing several cranial dimensions of the largest and smallest specimens of *Antrozous* (open squares) and *Bauerus* (solid circles) with *Auzanycteris* (the line at zero). The logs of the measurements of *Auzanycteris* are assumed to be zero, while the differences between the log of the measurements in the latter genus (standard) and genera being compared are plotted on the positive (+) or negative (—) sides of the zero line. The dimensions are as follows: 1 length of maxillary tooth row; 2 posterior end of m3 to posterior end of angular process; 3 APL C at cingulum; 4 W C at cingulum; 5 APL P4; 6 APL M1; 7 APL M2; 8 W talonid m1; 9 APL m2; 10 W trigonid m2; 11 W talonid m2; 12 APL m3; 13 W trigonid m3.

(by the temporal muscles) was calculated for the holotype and for all comparative specimens, and expressed as percentages of jaw lengths to eliminate size as a factor in comparisons. To quote from Ostrom (1966: 302-303): "It is not possible to measure this moment arm directly with any precision when the jaw is in articulation and fully adducted (the critical position), it must be calculated from other parameters taken from the skull and jaws." See Figure 7.

Ostrom continued: "For example: the moment arm of the applied force is a function of 1) the height (h) of the articulation, 2) the lever distance (a) between the center of the articulation and the base of the coronoid process [determined by the level of the center of articulation, above or below the level

of the toothrow] and 3) the attitude (angle θ) of the line of action of the applied force (F) relative to the fulcrum. . . . the moment arm of the applied force is calculated by $m = (\theta + \delta)\ d$ where m equals the length of the moment arm of the applied force, θ the angle between the applied force and the lever axis, δ the angle between the diagonal distance (d) from the coronoid apex to the center of the glenoid fossa and the lever axis." The length of the moment arm of the applied force is in direct proportion to the force applied to the mandible, and as such is a measure of the force itself.

The moment arm of the applied force (m) and the angle θ are greater in *Bauerus* than in *Antrozous* and *Anzanycteris*. This is thought to be related to the greater degree of the "bulldog" effect in *Bauerus* than in the other two genera.

Only the base of the coronoid process is known for *Anzanycteris*, but the slope of the anterior and posterior margins of the process are visible and match favorably the condition in *Antrozous*, but not *Bauerus*. The measurements of the moment arms expressed in percentages of mandible lengths are as follows: *Antrozous*—KU 11374, 29; KU 11373, 27; KU 63546, 28; KU 94363, 28; KU 94362, 26; KU 75891, 27; KU 76874, 25; KU 11179, 24; ISUM 7305, 26; AMNH 2159, 28 (calculated from Van Gelder, 1959: fig. 1B); *Bauerus*—AMNH 180841, 32; AMNH 180565, 31 (calculated from Van Gelder, *loc. cit.*: fig. 1A); *Anzanycteris*—LACM 19300: 22 (if θ is assumed to be 20 degrees) or 26 (if θ is assumed to be 50 degrees).

It can be inferred from Table 1 that *Nyctophilus* and *Bauerus* represent an adaptive type with a bulldog-like upturned rostrum as opposed to the condition in *Anzanycteris* and *Antrozous*. The length of the upper incisor relative to the length of the upper canine seems to vary inversely with the degree of upturning of the rostrum.

The bulldog-like upturning of the cheekteeth in *Bauerus* versus the downturning in *Antrozous* and *Anzanycteris* may be related to feeding habits. *Antrozous* is known to feed at times almost exclusively on flightless insects (Orr 1954). Although the feeding habits in *Bauerus* are unknown, it is possible that food is obtained exclusively in flight, the "bulldog" effect enabling a stronger hold on larger insects than *Antrozous* and presumably *Anzanycteris*.

The three genera are almost equally morphologically distinct from one another (Fig. 8). Study of the reproductive systems in the living forms of the subfamily Nyctophilinae probably would shed further light on their relationships.

The number and character of the lower incisors and the related character of the lower canine seem to provide clues to the diversification within the Nyctophilinae. *Nyctophilus* seems to be the most primitive genus in that it has three fully developed lower incisors, probably no indentation on the lower canine, relatively large M3, and an unreduced talonid on m3. From this primitive condition a morphological series develops, proceeding from *Nyctophilus* to *Bauerus* to *Antrozous* to *Anzanycteris*. Since *Anzanycteris* is known to occur only in the early Pleistocene, it is probable this diversification occurred sometime in the early or middle Tertiary.

Iguana, Hypolagus regalis, Perognathus, Geomys, Neotoma, and a small *Sigmodon* were found at approximately the same level and associated with *Anzanycteris*. A tropical or subtropical savannah is suggested by this faunal assemblage.

cf. **Anzanycteris** sp.
figure 6

LACM 19302 is a right maxillary fragment with P4-M3, and is not readily referable to any known genus. Here it is tentatively referred to *Anzanycteris* for the following reasons: (1) anterior to P4, the posterior and medial portion of the alveolus of the canine is visible and there is no evidence for the presence of a small premolar; (2) in all cheekteeth except P4, the dimensions are essentially as in *Anzanycteris*, P4 being markedly shorter antero-posteriorly (Table 2). Also the cingulum in M1 and M2 forms a prominence seen from an occlusal view, which projects from the center of each tooth, mediad.

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